7-1996

Female Choice in Sage Grouse: The Roles of Attraction and Active Comparison

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Published in *Behavioral Ecology and Sociobiology* 39:1 (July 1996), pp. 55–59;
doi: 10.1007/s002650050266

Submitted November 11, 1995; revised March 16, 1996.

Female Choice in Sage Grouse: The Roles of Attraction and Active Comparison

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Abstract
Previous studies of female choice in sage grouse *Centrocercus urophasianus* have implicated both the acoustic quality and repetition rate of the stereotyped strut display as putative cues for female choice. Stages in the choice process at which specific components of male courtship display influence female decisions were investigated using field observations of female premating behavior. Females visited a subset of territorial males and then actively chose one of these as a mate. The order in which males were visited suggested that females searched until an acceptable mate was found, rather than employing a "best-of-*n*" tactic. Numbers of females visiting a male were related to differences in an acoustical component of display (inter-pop interval) whereas the probability that a visiting female mated was related to display rate, indicating that initial attraction and active choice are influenced by different components of display. In addition, inter-pop interval and display rate tended to covary inversely, suggesting that attraction and active choice may impose conflicting selection pressures on display performance.

Keywords: sexual selection, passive attraction, active choice, constraints, sage grouse

Introduction

Much empirical research on mate choice during the past decade has been concerned with identifying traits that distinguish preferred from rejected males. By contrast, much less is known about the proximate mechanisms by which choices are made. Parker (1983) distinguished between passive attraction, in which some males are chosen more often because they are more easily detected by females, and active choice, in which particular individuals

are chosen after several have been inspected closely, and argued that the implicit complexity of the latter process provides evidence for adaptive choice. Since then several researchers have provided evidence for active female choice, principally in birds (Trail and Adams 1989; Dale et al. 1990, 1992; Petrie et al. 1991; Bensch and Hasselquist 1992; Choudhury and Black 1993; Hovi and Rätti 1994; Fiske and Kålås 1995; Rintamä ki et al. 1995), while others have proposed rules by which animals might compare potential mates (Janetos 1980; Wittenberger 1983; Real 1990; Dombrovsky and Perrin 1994). However, the relative importance of attraction and choice in sexual selection, the extent to which they favor the same versus different traits, and the proximate rules by which prospective mates are compared remain poorly known.

This paper presents data from a field study of sage grouse lek mating behavior that indicate that attraction and active comparison may select for different components of male courtship display. The sage grouse *Centrocercus urophasianus* has a short mating season in spring during which males display at traditional lek sites each morning. Females attend leks on a few (usually 2–3) days each season, visiting the territories of several males and typically mating once with the last male visited (Gibson and Bradbury 1986). While on their lek territories males repetitively perform a highly stereotyped display, the strut (Wiley 1973a), that contains conspicuous visual and acoustic components. Strutting rates peak when hens are on or near a male's territory. In previous studies (Gibson and Bradbury 1985; Gibson et al. 1991), we examined cues used by females in choosing mates by identifying factors that predict the distribution of mating among territorial lek males. Playback experiments were also used to explore the role of the acoustic components of display (Gibson 1989). This work has implicated aspects of display performance (particularly acoustical structure), prior mating experience and the choices of other females as cues. Additional cues, including the display rate, have been implicated in choice trials with captive birds (Boyce 1990; Spurrier et al. 1991, 1994). Here I present supplementary analyses of female premating behavior that examine the stages of pre-mating behavior at which particular components of male display influence choice.

Methods

Data on the premating behavior of females were collected at a lek (lek 4) in Long Valley, Mono County, California (37°40′N, 118°50′W) between 15 March and 30 April 1984, 1985, 1986, and 1989. This interval included the main period of lek display and mating activity in each year. The study area and observational methods have been described in detail previously (Gibson and Bradbury 1985; Gibson et al. 1991). In each year most territorial males at the lek were individually recognizable either because they were color banded or by idiosyncrasies in tail shape and the pattern of spotting on the under-tail coverts. More than 60 females were color banded over this period, but relatively few were seen at lek 4. Consequently, most females in this study were not banded. Unless many hens were present, unmarked individuals could be followed continuously throughout a morning (unlike some other lekking birds, female sage grouse do not make repeated visits to a lek within the same morning), but they were not identifiable from day to day.

To examine premating behavior, 40 females were followed from arrival at the lek to departure during single mornings. A total of 20 focal females (22.5% of all female lek days) were observed in 1984, 9 (6.7%) in 1985, 6 (2.4%) in 1986, and 5 (3.9%) in 1989. These observations were collected over 40 days starting 11 days before the seasonal onset of mating. Each bird's location was mapped at 1–2 min intervals as she walked (typically) or flew (occasionally) between different locations on the lek, and all occurrences of sexual behavior (solicitation and mating) and agonistic interactions with other females were noted. Later each individual's track was superimposed on a map of male territories (defined as the top 50% of a male's spatial utilization distribution: details in Gibson and Bradbury 1987) to determine the identities and order of males visited. A hen was judged to have visited a male's territory if she spent ≥ 2 consecutive sample points (effectively ≥ 2 min) within it; successive entries following visits to other territories were counted as additional visits. The 2-min criterion was adopted to include cases in which a female stopped near a male while he courted her and to exclude instances in which she moved through a territory without stopping and hence showed no apparent interest in the male. This occurred when females walked through closely packed intervening territories when moving from one male to another. Imposing the 2-min criterion does not qualitatively alter any of the conclusions reported, though as shown in the Results, it reduces the numbers of males that a female was judged to have visited by 35%. On each day we also recorded the peak number of males on the lek from counts taken throughout the morning and the number of territorial males present. The latter number is always lower because peak counts included a substantial number of nonterritorial males that move onto and off the lek with female arrivals and departures (Gibson, in press).

The influence of male display performance on both attraction and active choice was examined as follows. The effectiveness of each territorial male in attracting females was measured as the proportion of focal females that visited his territory (as defined above). The propensity of females to mate with a male after visiting his territory (active choice) was measured by first scoring whether or not at least one focal female mated with him, and then using logistic regression to partial out differences in the proportion of focal females attracted before testing the effects of specific display traits on mating probability. Mating was treated as a binary variable because no male was chosen by more than one focal female in any year. This reflects the small number of females sampled each year rather than an unusually low degree of mating skew at the study lek.

I analyzed the role of two aspects of male display performance, the acoustic quality and repetition rate of the strut display. Acoustic quality was measured by the interval between the two popping notes that terminate the strut display, a measure that was shown to vary individually and to be a consistent predictor of male mating success at the same lek by Gibson et al. (1991), who provide methodological details of sound recording and acoustic analysis. Mean values of inter-pop interval were computed from ten displays for each recorded territorial male.

Display rate was computed as the harmonic mean of intervals between 21 successive displays logged when females were on the lek (see Gibson et al. 1991 for details). Because most males display at higher rates when females are close to them (Wiley 1973b), these measures were corrected for female proximity as follows. Samples for each male (n = 8 to

30) were regressed on the distance between the male and the nearest female (square-root transformed), and then adjusted to a common distance of 5 m, representing the context in which a male is courting females on his territory. Although Wiley (1991) has suggested that a nonlinear correction may be more appropriate, polynomial models fitted the data better than linear regressions for only 7.5% of males, and in these exceptional cases using a polynomial model produced only trivial changes in adjusted display rate. Although display rate in this context was not a significant predictor of mating success in our earlier study, I considered it here because of its implication in short-range choice by captive sage grouse (Spurrier et al. 1994). Initially, I also analyzed the role of a second measure, display rate when hens are off a male's territory (at 50 m), which was implicated as a possible predictor of mating success by Gibson et al. (1991). However, because this had no effect on either attraction or mating probability independent of the measures already described, the results are not reported here. Finally, while display measures would ideally be measured simultaneously with observations of each female's movements, this was not practicable. Consequently, values for inter-pop interval and display rate used here are seasonal means. These measures were available for the years 1984 to 1986. No adjustments were made for stage of season, since none of the sampled males showed significant seasonal variation in display rate when investigated with linear or polynomial regressions.

The preceding measures were available for a subset of territorial males in each year. Because samples for each year were too small for individual analysis, data were combined across years after first checking that years were not statistically heterogeneous. Note that because of small sample sizes the power of the tests for heterogeneity is lower than those used in previous analyses of annual variation in mating success which showed significant variation in the effects of some other traits (Gibson et al. 1991). To ensure that relationships between male attractiveness and display measures reflected only within-year variation, the proportion of females attracted by each male, inter-pop interval, and display rate were each scaled as *z*-scores relative to their respective annual means and standard deviations before combining years.

Results

Female premating behavior

Observations of premating behavior suggest that female choice involves two stages, attraction to a subset of males followed by active choice among them. Table 1 summarizes numerical contrasts supporting this inference. On a daily basis, an average female traversed the territories of five or six males, and visited (see Methods) three or four of these. Visited males represented only 22.3% of territorial individuals and 14.3% of the peak count for the morning, which suggests that many males were rejected without being approached. Although the number of males visited could have been expanded by visiting different sets of individuals over several days, four individually marked females each followed over two or three mornings also visited relatively few males; 0–5 daily and 2–6 (mean ± SD = 4.3 ± 2.1) cumulatively. Of the 16 focal females observed mating, all but one mated with a single male; the exception mated with a second male after her first mating was aggressively dis-

rupted. Other visited males were apparently rejected after active comparison. An alternative interpretation, that visiting multiple males merely indicates low sexual motivation (Arak 1988), is inconsistent with the fact that hens that left the lek without mating, and which were presumably less motivated to mate, tended to visit fewer males (Table 1).

There was also wide variation around the mean patterns summarized in Table 1. Females visited from zero to ten males per morning at the lek and individuals that visited more males spent more time on the lek ($r = 0.703$, $n = 40$, $P < 0.0001$).

Table 1. Descriptive statistics for sampling behavior during single visits to the lek by focal females. With the exception of soliciting and mating, a hen's behavior while on the lek was not related to whether or not she mated (Mann-Whitney *U*-tests, alpha = 0.05)

Measure	Nonmating $n = 24$ mean (SD)	Mating $n = 16$ mean (SD)	All $n = 40$ mean (SD)
Males on lek:			
Peak count	27.2 (6.7)	25.4 (5.3)	26.5 (6.2)
Territorial males	16.2 (4.6)	18.0 (4.4)	16.8 (4.5)
Territories traversed	5.3 (4.4)	6.1 (3.7)	5.6 (4.1)
Territories visited	3.5 (2.7)	4.1 (2.4)	3.7 (2.6)
Territory visits	4.2 (3.7)	5.0 (2.9)	4.5 (3.4)
Males solicited	0.2 (0.5)	1.4 (1.0)	—
Males mated	0 (0)	1.1 (0.3)	—

Table 2 lists sequences of territory visits for the 16 focal hens that mated. These illustrate the relationship between premating visits and choice on the day of mating but do not necessarily include the complete premating history of each individual, some of which may have occurred on earlier days.

The sequence data show two patterns of interest. First, when males are ranked in order of first encounter (as in Table 2), a female was more likely to mate with the last individual encountered than with a male picked at random from those visited. Of 14 hens that visited more than one male, ten mated with the last encountered male whereas only 3.84 such cases are expected if order of encounter is not a factor (goodness of fit $\chi^2 = 13.643$, $df = 1$, $P < 0.001$). Second, hens commonly returned to males that they had visited earlier. Half of the 16 hens made return visits to at least one male, and this does not include unrecorded returns to males visited on a previous day. With the exception of one individual that twice returned to her eventual mate after being chased away by another female, all return visits were unforced. Of 17 return visits, 5 led to mating, 8 were followed by rejection, while 4 others were followed by another visit prior to mating or rejection.

Table 2. Sequences of visits to male territories on the day of mating by 16 females. Mating occurred on the last visit in each sequence (*underlined*). Males are numbered by order of first encounter. Initial visits are shown in *plain type* and revisits in **bold**.

1	1–2–3–**1**
1	1–2–**1**–3–**1**
1–2	1–2–3–**1**–**2**–**1**–**3**–**1**
1–2–3	1–2–**1**–3–4–5
1–2–3	1–2–3–4–5–**2**–**5**
1–2–3	1–2–3–4–**1**–**2**–5
1–2–3	1–2–3–4–**1**–5–6–**1**–**2**
1–2–3–4–5–6–7–8–9	1–2–3–4–5–6–**5**–7–8

Male display and levels of choice

Male display performance appeared to affect both initial attraction and active choice, but in different ways.

Males that were visited by more hens performed displays with longer inter-pop intervals but did not display at higher rates (Table 3). This suggests that vocalizations with longer inter-pop intervals were more effective in attracting hens to a male's territory, but that their repetition rate was not a factor. By contrast, after partialing out the proportion of hens visiting each male, the probability that a male mated increased with his display rate but not with inter-pop interval (Table 3). This suggests that active choice was affected by the rate at which a male displayed when females were nearby. As a check on the latter result, I compared chosen males with others that were visited but rejected by the same female. This comparison was possible for six females for which seasonal display rates (at 5 m) were known for the chosen male and at least half (mean ± SD = 71 ± 24%) of the others visited. Chosen males displayed at higher rates in five of the six cases, which is in the right direction, though the sample is too small to show a statistically significant effect (Wilcoxon matched-pairs signed-ranks test: $P = 0.109$).

Table 3. Relationships between two measures of male display performance and measures of (1) initial attraction (the proportion of focal females visiting a male) and (2) active choice (the probability that a male was mated by a focal female). Effects of display on mating probability were analyzed using logistic regression models after controlling for differences in initial attractiveness by including the proportion of hens visiting as a covariate.

Cue	% Hens visiting Kendall's τ	Mating probability partial *b'*	*n* (Males)
Inter-pop interval	0.374**	0.608	30
Display rate – 5 m	–0.143	5.438***	22

** $P < 0.01$, *** $P < 0.001$

If, as the preceding analyses suggest, females are attracted to males with longer inter-pop intervals but then reject those with lower display rates, the probability that a male mates should be affected by both inter-pop interval and display rate. Figure 1 confirms the

anticipated pattern. A logistic regression model shows significant partial effects for both display components (model fit: $\chi^2 = 13.106$, $df = 2$, $P = 0.0015$; inter-pop interval: $\chi^2 = 10.342$, $df = 1$, $P = 0.0013$; 5 m display rate: $\chi^2 = 15.889$, $df = 1$, $P = 0.00007$).

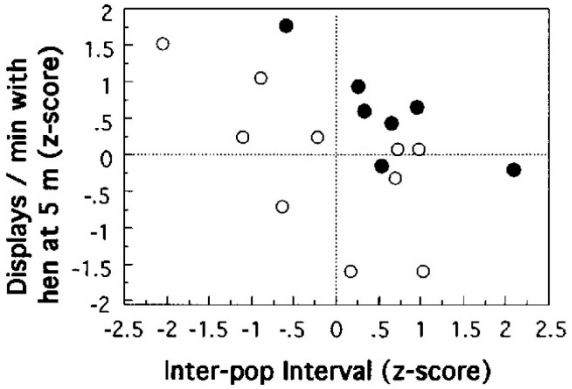

Figure 1. The relationship between inter-pop intervals, the rate at which males displayed to females at a range of 5 m, and whether or not a male was chosen by any focal female (*filled symbols* chosen, *open* not chosen)

Figure 1 also shows that display rates and inter-pop interval tend to covary inversely ($r = –0.455$, $n = 17$, $P = 0.066$). In an attempt to confirm this relationship, I also analyzed a larger sample of birds including data from 1987 when female premating behavior was not recorded. The correlation remained marginally nonsignificant ($r = –0.373$, $n = 28$, $P = 0.0503$).

Discussion

The data provide evidence that both attraction and active comparison play roles in female choice, and that females respond to different aspects of male courtship display performance at each stage. These results help to resolve some inconsistencies between previous studies of female choice in this system, bear on the general issue of how active choices are made, and raise the possibility that trade-offs between different components of display performance might limit display elaboration.

The inference that acoustic differences in male display affect long-range attraction is in line with experimental playbacks showing that the acoustic component of the strut display can attract females (Gibson 1989; Young 1994). Although the reason why displays with longer inter-pop intervals are more attractive is unknown, it may be related to their volume since sound pressure level in an octave band centered on 2 KHz is positively correlated with inter-pop interval (J. W. Bradbury, unpublished work). Louder displays might be more conspicuous to females either because of their greater radius of detection or increased conspicuousness against the acoustic background of other males. The implication that display rate plays a role in active choice also fits with observations of captive birds by Spurrier

et al. (1994). The present analysis also suggests why this effect was not detected in a previous field study that used numbers of matings as a measure of male attractiveness (Gibson et al. 1991). Where differences in long-range attractiveness make a major contribution to differences in male mating success, the effects of factors that influence the active choice decision are likely to be obscured, particularly if traits influencing decisions in each phase tend to be inversely related (Fig. 1). This interpretation points to the need to take the *process* of mate choice into account when attempting to identify the cues involved.

The recognition that different cues operate at different stages of the choice process may also resolve another inconsistency between recent field and captive studies. Gibson et al. (1991) found that a female's choice of mate is strongly affected by the choices of other females that mate on days when she is at the lek, whereas Spurrier et al. (1994) were unable to confirm this "copying" effect with their captive birds. In the field, males were more likely to attract females if they already had one or more females on their territory (Gibson et al. 1991) which suggests that the presence of other females affects initial attraction. If this were the primary mechanism behind mate choice copying, then the failure to observe copying when females were choosing between males in close proximity would not be surprising because the captive situation precludes long-range attraction and more closely resembles the active comparison context. This interpretation is in line with copying being the result of a tendency for females to aggregate rather than imitation of the mating decisions of others (McComb and Clutton-Brock 1994).

Most prospective theoretical treatments of active choice have modeled the process as one of sequential encounter (Janetos 1980; Real 1990; Dombrovsky and Perrin 1994). My data indicate that sequential encounter is a part of the process by which female sage grouse choose mates, even though differential attraction is also a factor and the close proximity of males also provides opportunities for simultaneous comparison. Sequences of territory visits also bear on the issue of whether females search using a threshold criterion or employ a best-of-n (pooled comparison) tactic, in which encountered males are retained pending a final decision (Real 1990). The bias toward mating with a male that is first encountered at the end of the sampling sequence argues for a threshold criterion and against best-of-n. Real (1990) showed that the former tactic yields a higher payoff if choice is costly. The fact that inspecting additional males takes more time is consistent with this idea, although time spent on leks entails only trivial increases in one cost component, predation risk (Gibson and Bachman 1992). Other features of the sequences are compatible with either threshold or best-of-n tactics and with additional processes. For example, revisiting previously encountered males for mating might be explained by either pooled comparison or a threshold model with a declining acceptance threshold. Alternatively, any unforced return visit might be a resampling tactic undertaken to collect additional information, as would be expected if discrimination is difficult and can be improved by additional observation (Getty 1995; Luttbeg, in press). Separating these possibilities is beyond the scope of the present study. However, because these patterns of revisiting are also characteristic of premating behavior in other birds (references cited in Introduction), further analysis of their causes would be of interest.

Finally, evidence that attraction and active choice involve different cues that tend to covary inversely, raises the intriguing possibility that that elaboration of each component

of display performance is constrained by the other. In other words, sexual selection via mate attraction may be opposed by selection via active choice. Although the negative relationship between display rate and inter-pop interval and display rate is not strong, it is also apparent in a recent comparison of acoustic structure and display rate among sage grouse populations (Young et al. 1994). If inter-pop interval constrains display rates, this could be because displays with longer inter-pop intervals take more time to perform or, for biomechanical or energetic reasons, require a longer recovery time. In view of its relevance to understanding limitations on the elaboration of sexual ornaments, this issue merits further study.

Acknowledgments – Paul Povey, Elizabeth Ross, and Wendy Binder, among others, made important contributions to data collection, and Gwen Bachman provided assistance at various stages of this work. The study was supported by grants from the NSF.

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